Modulatory effects of happy mood on performance monitoring: Insights from error-related brain potentials

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Abstract

Goal adaptive behavior requires the rapid detection of conflicts between actions and intentions or goals. While many studies have focused in the past on the influence of negative affect on this cognitive control process (and more specifically, on error monitoring), little is known about possible modulatory effects of positive affect on it. To address this question, we used a standard (positive) mood induction procedure (based on guided imagery) and asked participants to carry out a speeded Go/NoGo task, while high density EEG was recorded concurrently. As a control condition, we used a group with neutral mood. ERP results showed that the ERN (error-related negativity) component, reflecting early error detection within the dorsal anterior cingulate cortex, was not influenced by happy mood. In contrast, the subsequent Pe (error positivity) component, related to the appraisal of the motivational significance of errors, was reliably smaller in the happy relative to the neutral mood group. Complementing source localization analyses showed that this effect was explained by a decreased activation within the posterior cingulate and insular cortices. These results were obtained in the absence of group differences regarding behavioral performance and tonic arousal. These findings suggest that happy mood likely decreases and changes the motivational significance of worse than expected events (Pe), while leaving their earlier automatic detection (ERN) unaltered. We discuss these new results in terms of dynamic changes in the complex interplay of performance monitoring with motivation.

Modulatory effects of happy mood on performance monitoring:

Insights from error-related brain potentials

Human behavior is characterized by a high amount of flexibility, necessary to deal efficiently with rapidly changing demands in the environment. This ability stems from dedicated cognitive control mechanisms that monitor the occurrence of deviances between intended and actual actions, and if detected, trigger in turn specific remedial processes (Botvinick & Braver, 2015). In this framework, performance monitoring (PM) is usually achieved by the processing of external incentives (such as positive or negative feedback) or internal/motor cues (such as correct responses or response errors) (Ullsperger, Fischer, Nigbur, & Endrass, 2014). Feedback-locked and response-locked PM is thought to operate via dopaminergic-dependent reward prediction error mechanisms or signals influencing specific fronto-striatal loops in the human brain (Frank, Woroch, & Curran, 2005; Holroyd & Coles, 2002; Walsh & Anderson, 2012). Interestingly, accumulating evidence shows that PM is not immune to changes in the affective state of the participant or specific motivational drives (Koban & Pourtois, 2014; Olvet & Hajcak, 2008; Weinberg, Riesel, & Hajcak, 2012). More specifically, response-locked PM brain mechanisms appear to be reliably influenced by trait negative affect (as anxiety/apprehension/worry) (Moser, Moran, Schroder, Donnellan, & Yeung, 2013; Olvet & Hajcak, 2008; Pizzagalli, 2014), as well as induced negative emotion (Wiswede, Münte, Goschke, & Rüsseler, 2009; Wiswede, Münte, & Rüsseler, 2009). By comparison, much less is known about potential modulation of PM by emotions of positive valence. This paucity is somewhat surprising at first sight, given that positive emotions fuel resilience and well-being (Sheldon & King, 2001), and they are usually assigned a special, protective or beneficial, role in core cognitive processes, such as attention, reasoning or creativity (Fredrickson, 2001). Accordingly, in this study, we set out to test the prediction that positive emotions could perhaps influence PM, with a focus on early response-locked error monitoring processes, which were previously found to be susceptible to effects associated with negative emotions.

At the electroencephalographic (EEG) level, error monitoring provides a very good insight into PM processes and their malleability by affect or motivation, given that this process is captured by systematic amplitude variations of two well-documented event-related potentials (ERPs): the error-related negativity (ERN or Ne) and the error positivity (Pe) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Ullsperger, Danielmeier, & Jocham, 2014). While the ERN component reflects the early, perhaps automatic, detection of a discrepancy (in terms of motor representations) between the incorrect executed and the correct desired or intended action (Coles, Scheffers, & Holroyd, 2001; Gehring et al., 1993), the subsequent Pe is usually related to the conscious appraisal of response errors and/or the processing of their motivational significance (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Koban & Pourtois, 2014; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Ridderinkhof, Ramautar, & Wijnen, 2009). Hence, the ERN and Pe likely reflect two distinctive processes during error monitoring and PM more broadly defined.

Despite its ultra-fast neurophysiological time course (as it is usually elicited 0-100 ms after error commission over fronto-central electrodes along the midline), and high degree of automaticity, the amplitude of the ERN varies however with motivational factors (for example when accuracy is emphasized, see Gehring et al., 1993) or emotional variables (like trait anxiety, see (Aarts & Pourtois, 2010) suggesting that it is not only reflecting motor cognition per se, but probably already capturing emotional appraisal processes during PM (for a review see Olvet & Hajcak, 2008). For example, the ERN amplitude is usually increased for internalizing traits or disorders, including depression (Chiu & Deldin, 2007; A. J. Holmes & Pizzagalli, 2008), anxiety (Aarts & Pourtois, 2010; Hajcak, McDonald, & Simons, 2003a), and obsessive compulsive disorder (Endrass & Ullsperger, 2014). By comparison, its amplitude is usually decreased in externalizing traits or disorders, such as in subjects with cocaine dependence (Franken, van Strien, Franzek, & van de Wetering, 2007), or impulsive personality characteristics (Ruchsow, Spitzer, Grön, Grothe, & Kiefer, 2005). Growing evidence showing a reliable increase of the

ERN amplitude with negative affect at a non-clinical level (Hajcak, McDonald, & Simons, 2004; Luu, Collins, & Tucker, 2000; Vaidyanathan, Nelson, & Patrick, 2012) has been extended by studies examining manipulated sadness, short term negative affect and induced helplessness (Olvet & Hajcak, 2012; Pfabigan et al., 2013; Wiswede, Münte, Goschke, et al., 2009; Wiswede, Münte, & Rüsseler, 2009). All in all, these studies concur and suggest that negative affect (conceived either as a trait or a state) reliably increases the ERN component.

By comparison, the subsequent Pe component, peaking 145-300ms after error commission over more posterior central areas than ERN/Ne, considered to covary closely with the degree of error awareness or the amount of salience induced by response errors (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005), appears to be much less systematically influenced by negative affect. However, scattered evidence suggests that an overactive ERN usually goes along with a decreased Pe, as demonstrated in subjects reporting high levels of trait negative affect (Hajcak et al., 2004), in clinical depression (Aarts, Vanderhasselt, Otte, Baeken, & Pourtois, 2013; Chiu & Deldin, 2007; A. J. Holmes & Pizzagalli, 2010; Olvet, Klein, & Hajcak, 2010; Schrijvers et al., 2009; Schroder, Moran, Infantolino, & Moser, 2013), or in studies inducing threat as negative emotional state (Moser, Hajcak, & Simons, 2005). The lack of a clear understanding of effects of (negative) affect on the Pe is also reinforced by the fact that in many studies the authors usually focus on the ERN exclusively, but they do not report possible effects for the subsequent Pe component.

Although still debated in the literature, the enhanced ERN amplitudes accompanying negative affect most likely reflect higher significance of response errors for these subjects, i.e. they recruit more cognitive resources to detect errors, while the reduced Pe amplitude could reflect a lower awareness or salience of error commission, even though it appears then difficult to reconcile these two opposite accounts. At any rate, an overactive ERN in negative affect is in line with both the assumption of a mood congruency effect during PM(Rusting, 1998), as well as the divergent functional significance of specific

mood states (Fredrickson, 2001, 2004). In this latter framework, mood does not simply trigger changes in the approach vs. avoidance motivational system in a way which is compatible with the actual mood content (negative mood yields avoidance, while positive mood fosters approach). Instead, distinct mood states are characterized by different functions that can in turn influence cognition and behavior in non-transparent ways. According to this model, negative mood signals a potentially threatening environment, whereby the individual puts more efforts to timely detect and eventually avoid possible dangers or threats. Presumably, unwanted response errors are aversive and belong to this category, and their swift detection at the ERN level may therefore be gated with the encounter or experience of negative affect. In contrast, positive mood signals a safe environment, where a more creative and heuristic processing style is usually promoted, leading to a broadening of attention and the building of (additional) mental resources (Fredrickson, 1998, 2001). Therefore, in a happy mood state, there is no need for increased error monitoring. Further, this state likely shields the individual from experiencing negative affect or distress when encountering worse than expected events, and as such, it helps to maintain the current and pleasurable mood state (Schwarz & Bless, 1991). However, whether or not the latter affective state (positive mood) leads to a change in the amplitude of the ERN or Pe remains unsettled. As a matter of fact, discrepant findings have been reported in the past regarding modulatory effects of positive affect onto early error monitoring processes at the ERN level, while results for the Pe amplitude were usually not scrutinized or reported. Some studies reported smaller ERN amplitude related to higher life satisfaction (Larson, Good, & Fair, 2010), religiosity, which is linked to a general positive view on life (Inzlicht, McGregor, Hirsh, & Nash, 2009), or to positive affect after watching movie clips (van Wouwe, Band, & Ridderinkhof, 2011). In other studies the opposite pattern was sometimes found: Wiswede et al. (2009) found a larger ERN in a Flanker Task, when the stimuli were overlaid on pleasant IAPS pictures; Bakic, Jepma, De Raedt, & Pourtois (2014) found a larger ERN amplitude during a probabilistic learning task after positive mood induction with guided imagery. Moreover, other studies

actually failed to find reliable influence of positive emotions on the size of the ERN component (e.g. Luu et al., 2000 where positive affect was assessed using the PANAS). This discrepancy likely stems from the fact that different methods to induce and measure positive emotions or mood (in a very broad sense) have been used across these different studies. To measure mood, verbal self-reports or subjective ratings are often applied, but they show specific limitations, such as introspection, unlike more objective psychophysiological measurements. To induce a positive emotional state, very often automatic emotional reactions are provoked using specific emotional material (pictures, music, films) or rewards/punishments (for a review see Gilet, 2008; Westermann et al., 1996). However, because the same material is used for all subjects (to seek standardization), it lacks individualization and may therefore be suboptimal. For this reason, more recently, induction techniques based on the use of guided imagery and the recall of personal autobiographical information have been proposed as alternatives to overcome this limitation and eventually induce more potent subject-specific mood states with enhanced ecological validity (Bakic et al., 2014; E. A. Holmes, Mathews, Dalgleish, & Mackintosh, 2006; E. A. Holmes, Oughtrey, & Connor, 2008; Kross, Davidson, Weber, & Ochsner, 2009; Vanlessen et al., 2012; Vanlessen, De Raedt, Mueller, Rossi, & Pourtois, 2015; Vanlessen, Rossi, De Raedt, & Pourtois, 2014).

The goal of this study was to gain insight into possible modulatory effects of positive mood (once it is induced and maintained) on error monitoring, with a focus on the ERN and Pe ERP components. To this aim, we directly manipulated the current mood state of the participants by means of guided imagery (E. A. Holmes et al., 2006, 2008), while they performed a standard speeded Go/NoGo task/procedure. This task is suited to unlock a large number of unwanted response errors, and has been previously validated in a number of studies (Aarts, De Houwer, & Pourtois, 2012; Aarts et al., 2013; Aarts & Pourtois, 2010; Vocat, Pourtois, & Vuilleumier, 2008). The elected mood induction procedure (MIP) was validated in our laboratory across different studies (see Bakic et al., 2014; Vanlessen et al., 2014,

2013). Using it, we induced either a happy or a neutral mood in a between-subjects design. Once induced, participants carried out a speeded Go/NoGo task, while 64-channel EEG was recorded concurrently, to study the neurophysiology of error monitoring (ERN and Pe components) carefully. The "broaden and build" theory for positive emotions (Fredrickson, 2004) provides an important framework from which some predictions could be derived in the present case. In this framework, positive mood is thought to increase creativity (Isen, 2008; Subramaniam, Kounios, Parrish, & Jung-Beeman, 2009), cognitive flexibility (Nadler, Rabi, & Minda, 2010), and broaden attention (Vanlessen et al., 2012, 2014), while it can also impair specific components of executive functions, like planning, task switching and inhibition abilities (Mitchell & Phillips, 2007), because of the enhanced distractibility accompanying this specific mood state (Dreisbach & Goschke, 2004). Hence, in light of this evidence positive mood could very well interfere with, rather than increase, performance (accuracy, speed), early error monitoring processes and behavioral adaptation following error commission (i.e., post-error slowing). This might eventually be translated in a blunted ERN or Pe component during the rapid monitoring of response errors in individuals experiencing happy mood, compared to an active control condition with a neutral mood content. Besides the changes in the current mood state captured by subjective ratings, we also measured physiological arousal concurrently to assess whether modulatory effects of positive mood on error monitoring were related to changes in the autonomic nervous system or not.

Methods

Participants

Fifty undergraduate students from Ghent University took part in the study in exchange for 30 Euro compensation. All of them were right-handed, reported normal or corrected-to-normal vision, and had no history of psychiatric or neurological disorders. The study was approved by the local ethics committee and all participants gave written informed consent prior to participation. Participants were

randomly allocated to either a positive or a neutral mood condition (n = 25 per group). The data of three subjects were excluded due to failures of the mood induction (see Bakic, De Raedt, Jepma, & Pourtois, 2015; Bakic et al., 2014): within the neutral mood condition, two participants were excluded because their level of happiness increased and stayed on a very high level after the MIP compared to the rest of the neutral group (more than 1.8 *SD* above the mean), while within the happy mood group the data of one subject had to be excluded due to a decrease in levels of happiness following the mood induction compared to the baseline measurement prior to it (1.8 *SD* below the mean). Further, three participants (two of the happy group) had to be excluded due to technical problems during EEG data acquisition. Hence, 22 participants per mood group were eventually included in the final sample. These two groups were matched for gender and age (happy group M_{age} = 21.8 years, *SD* =2.52, 14 females; neutral group M_{age} = 22.4 years, *SD* = 2.26, 15 females).

Mood Induction

A previously validated mood induction procedure (MIP) was used (see Bakic et al., 2014; Vanlessen et al., 2014, 2012). In a between-subjects design either positive or neutral mood was induced by means of an imagery procedure in which participants were instructed to vividly imagine and re-experience a specific autobiographical memory episode (E. A. Holmes et al., 2006, 2008). Participants were kept naive regarding the purpose of the procedure as they were told it was about episodic memory abilities (and not about emotional re-experiencing). Prior to the MIP, participants were trained in multisensory imaging from their own perspective with a standard four step imagery exercise (manipulating a lemon) (E. A. Holmes et al., 2006, 2008). Then they had to choose an appropriate episodic memory that happened at least one week before, and that either made them feel very happy (positive mood group), or did not elicit any specific emotions but was linked to a physical activity (neutral mood group). We chose this specific instruction in the neutral mood group to try to balance levels of arousal (after the MIP) with the happy mood group (where usually both valence and arousal

increase, see Bakic et al., 2015). Table 2 provides a summary of the main memory contents retrieved by the participants, which shows that in the neutral group they mainly recalled sport-related activities, while in the positive mood group, they used activities characterized by the presence of a social component primarily. Next, the participants closed their eyes and tried to imagine the situation as vividly as possible two times for 60 seconds, intersected by precise questions asked by the experimenter about sensations and details, in order to encourage concrete imaginations (E. A. Holmes et al., 2008; Watkins & Moberly, 2009) and to ensure that regardless of the mood condition, they engaged similarly into vivid mental imagery. Finally, participants were asked (based on a rating scale with five points, ranging from 'not at all' to 'completely') how well they could imagine the situation using their own perspective, this was used as a short manipulation check to assess how strongly they could re-experience the desired memories (in their mind's eyes).The MIP was repeated after each block of the Go/NoGo task (every five minutes, three times) with the aim to maintain the targeted mood state throughout the whole experimental session.

To check (at the subjective level) the current mood state before the first and after every MIP, participants were asked to mark on a 10-cm horizontal visual analog scale (VAS) their current feeling of happiness, pleasantness and sadness. The left anchor was labeled with "*neutral*" and the right one with "*as happy/pleasant/sad as I can imagine*". Furthermore, participants had to rate their current arousal level with the Self-Assessment Manikin for Arousal (Bradley & Lang, 1994).

Task

Participants performed a modified version of a speeded Go/NoGo task that was previously used and validated in different studies (Aarts et al., 2013; Pourtois, 2011; Vocat et al., 2008), see Figure 1 for an overview. Visual stimuli consisted of a square or a diamond presented in the center of a white screen. Each trial started with a fixation cross (1000 ms), then a black square or diamond was presented for a variable time interval (between 1000 – 2000 ms to keep uncertainty of the target time high). Then this

geometric figure became either green or orange, while its in-plane orientation remained either identical (square-square or diamond-diamond sequence) or swapped (square-diamond or diamond-square sequence).This visual stimulus remained on the screen for 1000 ms or till a button press. Participants had to perform a speeded color plus shape discrimination task, where both speed and accuracy were emphasized. When the geometric figure turned green and kept its original shape (two third of the trials; Go trials), participants had to press a pre-defined key on the response box as fast as possible with their right index finger. If the geometric figures turned orange (one sixth of the trials) or changed shape (one sixth of the trials; all corresponding to NoGo trials), then they had to withhold responding. To ensure that every participant would commit a sufficient number of response errors (i.e., false alarms on NoGo trials) without creating excessive frustration or blurring task rules however, we used a strict reaction time cutoff (see also Aarts et al., 2012; Aarts & Pourtois, 2010; Vocat et al., 2008). On each and every (Go) trial, the reaction time (RT) was compared against an arbitrary cutoff. If the RT speed was above this limit (Slow hit trial, SH), then a negative feedback was provided 1000ms after response onset ("*too slow*" written in Dutch was presented for 500 ms in the center of the screen). No feedback was provided after a so-called Fast hits (FH, i.e., the RT speed was below the cutoff) or errors, to increase internal monitoring in these cases. Unknown to the participants, this cutoff was calculated during specific calibration blocks that preceded each time the experimental blocks. During the first three experimental blocks, participants had to be 10% faster than the mean calculated during the (yoked) calibration blocks, and 20% during the last (fourth) experimental block. The added value of this procedure is that the RT cutoff is calculated for each participant separately and adjusted during the experimental session to deal with the inherent inter-individual variability in RT speed, as well as unspecific effects of time and habituation/learning (intra-individual variability; see Vocat et al., 2008). The experiment consisted of a practice block of 12 trials (four Go trials, four NoGo trials of each type), two calibration blocks of 14 trials (ten Go and two NoGo trials of each type), and four experimental blocks of 84 trials each. Each

calibration block was followed by two test blocks. Trial presentation was randomized within blocks. Stimuli were shown on a 21-in CRT screen, and the task was programmed and executed using E-Prime (V 2.0, Psychology Software Tools Inc., Sharpsburg, PA).

Recording and Preprocessing of Electrophysiological Data

EEG was recorded using a 64-channel Biosemi Active Two system (http://www.biosemi.com). EEG was sampled at 512 Hz and referenced to the Common Mode Sense (CMS) active electrode–Driven Right Leg (DRL) passive electrodes. The EEG was preprocessed offline with Brain Vision Analyzer 2.0, using a standard scheme of data transformation meant to extract response-locked ERPs (Keil et al., 2014). First, a 0.016 Hz high pass filter was applied, and the data were re-referenced using the common average of all electrodes[1]. Individual epochs were segmented using a ± 500 ms interval around the response onset. Eye blinks were removed automatically with the ocular correction for blinks (Gratton, Coles, & Donchin, 1983), using the difference amplitude of the two electrodes attached above and below the left eye respectively. Each epoch was baseline corrected using 200 ms time interval (-500 to -300 ms prior to the response). Artifact rejection was based on a ±70µV amplitude cutoff. Using this criterion, at least 70% of the individual segments were kept and included in the averages, with no significant group difference in the amplitude cutoff ($M_{Positive}$ = 72.6, *SD* =9.29, $M_{Neutral}$ = 75.2, *SD* = 9.82, $t(1, 42) = .915$, $p=.37$, $d = 0.27$). Individual trials were averaged separately for each condition, and finally, a 30 Hz low pass filter was applied before grand average response-locked ERP waveforms were computed.

[1] We performed additional analyses showing that the use of average mastoids, as opposed to the common average reference (see Supplementary Figure 1), did not change the main outcome of the study (i.e., happy mood influences the Pe component selectively).

Electro dermal activity (EDA) was recorded continuously (512 Hz sampling rate, using the same parameters as for the EEG recording) via two bipolar electrodes that were attached to the volar surfaces of the distal phalanges of the left index and middle finger (of the non-dominant hand). Participants were instructed to comfortably lay their left forearm on the table, and were asked to not move it during the experimental blocks.

Data Analysis

Analysis of mood manipulation effects & behavioral data.

For these and all subsequent analyses, the significance alpha cutoff was set to 0.05. To check for the efficiency of the MIP, a mixed model ANOVA with mood (positive vs. neutral) as between-subjects factor and time (5 MIP ratings) as within-subject factor was used, separately for all four assessments (happiness, pleasantness, sadness, and arousal). Whenever the two-way interaction was significant, it was followed up by independent sample t-tests calculated for each time point to compare mood levels between the two groups across the experimental session. Additionally, paired sample t-tests between the successive time points for each mood group separately were carried out to assess the strength and direction of the mood change resulting from the MIP. To assess if imagination abilities or involvement in the (guided imagery) task differed between groups, a mixed model ANOVA with mood as between-subjects factor and time (5 measurement points) as within-subject factor was used.

For the main task, errors for the two NoGo trial types (color and orientation) were collapsed (see also Aarts & Pourtois, 2010, 2012), while only FH (corresponding to correct and fast, i.e. RT below the updated cutoff, decisions on Go trials) were used as correct responses for comparison purposes with incorrect ones. Accuracy and RT speed was compared between the two mood groups by means of independent sample t-test. The post-error slowing effect(Laming, 1979; Rabbitt, 1966) was also computed by comparing the two mood groups with a mixed model ANOVA with mood (positive vs.

neutral) as between-subjects factor and post-trial type (hits following errors vs. hits following FHs) as a within-subject factor.

Analysis of ERPs

We analyzed two error-related components: the ERN/Ne and the subsequent Pe component (Falkenstein et al., 2000; Gehring et al., 1993). The ERN is a negative deflection reaching its maximum amplitude over fronto-central electrodes along the midline (electrodes Fz and FCz), usually peaking 0 – 100 ms after (incorrect) response onset. The Pe is the positive deflection following the ERN, and it usually peaks around 150-300 ms post-response onset, with the maximum amplitude reached over central locations along the midline (electrode Cz). Based on the electrophysiological properties of the current ERP data set (see Figure 2A an 2C), the ERN was defined as the mean amplitude during the 10-60 ms post-response interval at electrode FCz. The Pe was calculated as the mean amplitude during the 145-205 ms interval following response onset at electrode Cz. For each ERP component separately, a mixed-model ANOVA with mood as between-subjects factor and accuracy (error vs. FH) as within subject factor was used. To control for arousal-related effects on these two response-locked ERP components, an additional ANCOVA was calculated with the same experimental factors, including the mean skin conductance level (SCL) as a covariate. To estimate if the current study was sufficiently powered to detect any group difference, post-hoc G*power analyses (Faul, Erdfelder, Lang, & Buchner, 2007) were performed.

Topographical analysis.

The classical peak analysis outlined here above was supplemented by a standard topographical ERP mapping analysis in order to characterize the topography (i.e., the actual geometrical configuration of the electric field defined by all 64 channels concurrently) of these two main response-locked ERP components (ERN and Pe), and eventually assess effects of positive mood. All these analyses were carried out using CARTOOL software (Version 3.34; developed by D. Brunet, Functional Brain Mapping

Laboratory, Geneva, Switzerland). The basic principles of this method have been described extensively elsewhere (Michel, Seeck, & Landis, 1999; Murray, Brunet, & Michel, 2008; Pourtois, Delplanque, Michel, & Vuilleumier, 2008). First, using the K-means cluster analysis (Pascual-Marqui, 2002), the dominant topographical maps were identified, using the whole ERP epoch (i.e., from 500 ms before till 500 ms after response onset, corresponding to 512 time frames at a 512 Hz sampling rate), including the ERN and Pe components. Next, using spatial fitting procedures, the dominant topographies identified in the preceding step were then fitted back to the individual ERP data/average to determine their expressions across subjects and conditions. We used the global explained variance (GEV) as dependent variable, which corresponds to the goodness of fit of these dominant topographical maps. Finally, these GEV values were entered in an ANOVA with accuracy and map configuration as within-subject factors, and mood as between-subjects factor.

Source localization.

To estimate the configuration of the neural generators underling the previously identified error-related field topographical components, a distributed linear inverse solution was used, namely standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002). SLORETA solutions are computed within a three-shell spherical head model coregistered to the MNI152 template (Mazziotta et al., 2001). SLORETA estimates the 3-D intracerebral current density distribution within a 5-mm resolution (6239 voxels each with an equivalent current dipole). The 3-D solution space is restricted to the cortical gray matter and hippocampus. The head model uses the electric potential field computed with a boundary element method applied to the MNI152 template (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002). Scalp electrode coordinates on the MNI brain are derived from the international 5% system (Jurcak, Tsuzuki, & Dan, 2007). The calculation was based on the common average. The inverse solution results for the ERN and the Pe component were compared between the two mood groups using independent sample t-tests performed on log-transformed data. We used a

stringent nonparametric randomization test (relying on 5000 iterations) to reveal potential group differences in the inverse solution space through direct statistical comparisons between conditions and mood groups, setting the level of significance for all the analyses to $p < .01$ (see also Schettino, Loeys, Delplanque, & Pourtois, 2011; Schettino, Loeys, & Pourtois, 2013).

Analysis of skin conductance.

EDA was analyzed using Ledalab software V.343 (Benedek & Kaernbach, 2010a, 2010b), implemented in MATLAB (Version R2014a). Data were smoothed by convolution with an 8 point Gaussian window and a low-pass Butterworth filter of 5 Hz was applied. Artefacts were identified and interpolated using visual inspection (M = 1.34 %, SD = 3.02 %). Ledalab returns the SCL as a continuous measure of tonic EDA and separates it from a phasic driver underlying the skin conductance data as a continuous measure of phasic EDA or skin conductance responses (SCR). While SCL represents the global electro dermal level, SCR reflects the physiological response to certain events (here with a focus on responses, either correct or incorrect) superimposed to that (Benedek & Kaernbach, 2010b). The mean SCL for each and across all blocks (lasting for five minutes) was calculated per subject. Additionally, phasic SCR was quantified within a response window of 0.5 to 3.5 s after response onset, and with a minimum amplitude criterion of 0.05 µS (Boucsein et al., 2012). Individual data (average phasic driver for each epoch) were range corrected using the largest and lowest response per subject following the recommendation of Lykken and Venables (1971) before averaged for each condition. Changes of the SCL between the two mood groups were compared using a mixed-model ANOVA with mood as between-subjects factor and task block number (n = 4) as a within-subject factor. Changes in the SCR to different responses were also compared using a mixed-model ANOVA with mood as a between-subjects factor and accuracy as a within-subject factor.

Results

Manipulation Checks

There was a significant interaction of time and mood for all subjective ratings, except sadness ($F(4, 168) = 1.88$, p=.12, $\eta^2 = .040$); happiness: ($F(4, 168) = 23.5$, p <.001, $\eta^2 = .26$); pleasantness: ($F(4, 168) = 9.80$, p <.001, $.\eta^2 = .17$); arousal: ($F(4, 168) = 7.69$, p <.001, $\eta^2 = .15$. No significant group differences for mood ratings were found at baseline, prior to the first MIP, for none of the different ratings used (all $ts(42) \leq 1.57$, $p \geq .10$). After the MIP, only the positive mood group showed increased levels for happiness, pleasantness and arousal compared to baseline ($t(21) \geq 3.3$, $p \leq .003$), and showed higher levels of happiness, pleasantness and arousal compared to the neutral mood group for all successive time points (all $t(42) \geq 3.3$, $p < .020$).

Behavioral Results

Task performance was similar between the two groups (see Table 1): the error rate was not different between them ($t(42) = 0.11$, $p = .91$, $d = 0.034$). Likewise, the ratio between fast versus slow hits was similar ($t(42) = 0.89$, $p = .38$, $d = 0.027$). Moreover, the correlation between speed and accuracy was also balanced between the happy and the neutral mood group ($r_{Neutral}(20) = -.72$, $p < .001$, $r_{Happy}(20) = -.54$, $p = .009$; $Z = 0.95$, $p = .34$). The groups did not differ in RT speed either (for none of the trial type considered, see Table 1), nor in the individual time limit used to demarcate FH from SH ($t(42) = 0.027$, $p = .978$, $d = 0.001$). A classical post-error slowing effect was observed. RTs were longer for hits after an error compared to hits following a FH ($F(1, 42) = 22.1$, $p < .001$, $\eta^2 = .35$). However, the magnitude of the post-error slowing effect was not influenced by mood (main effect of mood: $F(1, 42) = 0.49$, $p = .49$, $\eta^2 = .008$; interaction mood and accuracy: $F(1, 42) = 0.18$, $p = .67$, $\eta^2 = .004$).

Manipulation check of the MIP did not reveal any significant group difference for the imagination abilities ($F(1, 42) = 0.06$, $p = .807$, $\eta^2 < .001$). This null finding therefore suggests that both

groups were equally strongly involved in visual imagery, ruling out thereby a strong asymmetry between them regarding (cognitive) load or efforts made to relive actively the targeted memory.

ERP Results

The analysis performed on the mean ERN amplitudes at FCz electrode showed a significant main effect of accuracy ($F(1, 42) = 45.33$, $p < .001$, $\eta^2 = .51$), but no significant effects of mood ($F(1, 42) = 1.34$, $p = .25$, $\eta^2 < .001$), or interaction between these two factors ($F(1, 42) = 1.33$, $p = .26$, $\eta^2 = .016$). The amplitude of the ERN (for errors) was larger than the amplitude of the CRN (correct-related negativity, for correct responses), see Figure 3A. Entering the mean SCL as a covariate revealed no significant effect ($F(1, 41) \leq 1.33$, $p \geq .26$, $\eta^2 \leq .031$). Post-hoc power estimations confirmed that the current study was sufficiently powered to detect a group difference at the ERN level ($1- \beta = 0.89$).

For the Pe component recorded at Cz electrode, the analysis showed a significant main effect of accuracy ($F(1, 42) = 75.99$, $p < .001$ $\eta^2 = .62$). Importantly, the main effect of mood ($F(1, 42) = 8.74$, $p = .005$, $\eta^2 = .17$) and the interaction between these two factors ($F(1, 42) = 4.13$, $p = .049$, $\eta^2 = .034$) were also significant. When the mean SCL was added as a covariate, the main effect of mood ($F(1, 41) = 8.52$, $p = .006$, $\eta^2 = .17$), and the interaction between accuracy and mood ($F(1, 41) = 4.50$, $p = .040$, $\eta^2 = .092$) remained significant. The Pe amplitude for errors was larger than the amplitude of the positivity related to correct responses (Pc) in both groups (neutral: $t(21) = 7.23$, $p < .001$, $d = 1.48$, happy: $t(21) = 4.99$, $p < .001$, $d = 0.98$), but this difference was reduced in the happy group. More specifically, while the Pc was only trend significant lower for happy than neutral participants ($t(42) = 2.04$, $p = .047$, $d = 0.61$), the Pe was clearly blunted in the happy compared to the neutral mood group ($t(42) = 3.07$, $p = .004$, $d = 0.93$), see Figure 3B. Post-hoc power estimations confirmed that the current study was sufficiently powered to detect a group difference at the Pe level ($1- \beta = 0.99$).

Skin Conductance Results

The ANOVA performed on the SCL values did not reveal any significant change of tonic arousal during the experiment (main effect of task block: $F(3, 126) = 0.79$, $p = .50$, $\eta^2 = .019$), or any difference between the two mood groups (mood: $F(1, 42) = 0.017$, $p = .89$, $\eta^2 < .001$, or the interaction task block and group: $F(1,126) = 0.11$, $p = .96$, $\eta^2 = .003$). However, an analysis performed on the phasic SCR to either error or FH did reveal a significant difference between these two opposite response types ($F(1, 42) = 6.44$, $p = .015$, $\eta^2 = .14$), with, as expected, a higher SCR for errors than for FH ($t(43) = 2.56$, $p = .014$, $d = 0.29$; $M_{FH}=.068$, $SD_{FH}=.059$, $M_{Error}= .091$, $SD_{Error}=.096$). The SCR was not globally influenced by mood ($F(1, 42) = .44$, $p = .51$, $\eta^2 = .01$), and the interaction between mood and accuracy was not significant ($F(1, 42) = .13$, $p = .72$, $\eta^2 = .001$).

Topographical Mapping Results

A solution with seven dominant maps explained 99.0 % of the variance. During the time interval of the ERN (10-60 ms post-response onset), a main topographical change between errors and FH was evidenced. While the topography of the ERN (errors) was qualified by a clear negative deflection at fronto-central electrode positions (around FCz), the CRN map (FH) was characterized by a weaker and broader prefrontal negative deflection (see Aarts & Pourtois, 2010; Aarts et al., 2013 for similar results with the same task), see Figure 2BC.

The ANOVA run on the GEV values obtained for each component (ERN/CRN) revealed a significant interaction between accuracy and map configuration ($F(1, 42) = 20.41$, $p < .001$, $\eta^2 = .13$). While the CRN map explained more variance for FH than errors ($t(43) = 4.89$, $p < .001$, $d = 0.86$), the exact opposite pattern was found for the ERN map ($t(43) = 3.57$, $p < .001$, $d = 0.56$). This effect was not modulated by mood, however (mood: $F(1, 42) = 3.52$, $p = .068$, $\eta^2 = .07$, any interaction with mood: $F(1, 42) < 0.62$, $p > .44$, $\eta^2 < .01$), see Figure 4AB.

During the Pe time interval (145 to 205 post-response onset), a specific error-related topography could be evidenced alike. It was characterized by a large positivity surrounding the Cz electrode position (Pe), while FH elicited a weaker and broader posterior positivity (Pc). Consistent with the observation that mood influenced the Pe when considering the amplitude of this component at electrode Cz, the ANOVA run on the GEV values obtained after fitting (hence reflecting the topography of this mid latency error-related ERP component) revealed a significant interaction between accuracy, map and mood (F(1, 42) = 4.61, p=.038, η^2= .03). As it can be seen from Figure 4, the variance of the topography elicited by FH in the neutral group could be explained better with the topographical map of the Pc (t(21) = 3.56, p = .002, d = 0.97) and for errors with the Pe topographical map (t(21) = 4.40, p < .001, d = 1.03), while there was no such differentiation in the happy group for the Pe map (t(21) = 1.77, p = .091, d = 0.43), but for the topographical map of the Pc (t(21) = 2.31, p = .031, d = 0.35), see Figure 4CD.

Source Localization Results

The statistical comparison in the inverse solution space between errors and FH within the time window of the ERN/CRN (10-60 ms post-response onset) revealed widespread clusters with stronger activation for errors compared to FH: one located within the midcingulate/anterior cingulate cortex (ACC) (including Brodmann Area (BA) 24, 32; max. at 5x, 40y, 5z; 32; BA 24; t(43) = 2.98, p = .003) and another one corresponding to the left frontal gyrus (FG) (including BA 7-11, max. at -15x, 50y,10z; BA 7; t(43) = 2.63, p = 0.007), see Figure 2D. However, mood did not influence these effects (group comparison for errors at ACC: t(42) = 0.16, p = .44; at FG: t(42) = 0.38, p =.35; group comparison for FH at ACC: t(42) = 0.40, p = .34; at FG: t(42) = 0.35, p =.36).

During the time interval corresponding to the Pe component (145-205 ms post-response onset), the statistical comparison between errors and FH showed that errors led to a stronger activation in a broad cluster extending from anterior/posterior parts of the cingulate gyrus (including BA 23, 24, 30-32; max. at 5x, -10y, 30z, BA 24; t(43) = 8.0, p< 0.001) to frontal (including BA 2-7, 18, 19, 37, 40) and

parietal regions (including BA 8-11, 20-22, 39). Further, a bilateral cluster within the insula with stronger activation for errors than FH was found (BA 13, max. at -35x, -25y, 20z, $t(43) = 7.89$, $p < 0.001$), Figure 2D. Importantly, a direct statistical comparison between the two mood groups for errors confirmed an alteration of the intracranial generators giving rise to the Pe: in the happy mood group, decreased activations (relative to the neutral mood group) within the posterior part of the cingulate cortex spreading to superior frontal and parietal gyrus (including BA 3-6, 8, 24, 31; max. at -5x, -10y, 70z, BA 6; $t(42) = 4.13$, $p < 0.001$), as well as the insula bilaterally (with an effect more pronounced in the right hemisphere, max. at 45x, -15y, 15z, BA 13; $t(42) = 3.29$, $p < 0.001$) were observed. By comparison, only very few nodes in the posterior parietal cortex showed a small difference between the two mood groups for FH (max -20x, -55y, 70z, BA 7; $t(42) = 2.79$, $p = .007$), see Figure 5.

Discussion

To explore possible modulatory effects of positive mood on error monitoring processes, we induced either a happy or a neutral mood (using a guided imagery technique) in healthy participants (unselected university undergraduates). After the MIP, all participants performed a speeded Go/NoGo task while 64-channels EEG and SCL (as a measure of autonomic arousal) were recorded concurrently. We chose this specific task because it allows to unlock a large number of response errors in each and every participant within a relatively short period of time, thereby facilitating its combination with an orthogonal mood manipulation (Bakic et al., 2015, 2014; Vanlessen et al., 2012, 2015, 2014). Moreover, this task is suited to examine and characterize, using scalp EEG methods, the neurophysiology of error monitoring, with the generation of two clear-cut and well-documented response-locked ERP components observed after error commission in this task, namely the ERN/Ne and the Pe (Aarts & Pourtois, 2010; Pourtois, 2011; Vocat et al., 2008). More specifically, we sought to assess whether experimentally induced positive mood could alter one (or both) of these two ERP components, in the opposite direction compared to

effects usually created by negative affect (when conceived as a state or mood effect at the subclinical level) or internalizing traits and psychopathology (for which the ERN is usually found to be overactive, while the subsequent Pe is decreased, compared to neutral mood; see Koban & Pourtois, 2014; Weinberg, Kotov, & Proudfit, 2015). Our new results show that positive mood decreases selectively the Pe component, while leaving the preceding ERN/Ne component unchanged (relative to an active control condition with a neutral mood content), suggesting a component-specific effect triggered by the happy mood state during error monitoring. Importantly, this effect was evidenced in the absence of obvious differences at the behavioral level between the two mood groups for both task performance and post-error adaptation. Likewise arousal did not differ between the two groups. Moreover, by using complementing topographical and source localization methods, we could gain insight into the actual neurophysiological expression of this selective change at the Pe level, as well as the underlying neural sources likely giving rise to it. Here below, we discuss the implications of these new results in greater detail.

The MIP used in this study led to the elicitation of a specific mood or emotional state characterized by a high level of experienced happiness and pleasure (positive emotion dimension) while leaving sadness (as negative affective dimension) unchanged. Moreover, we found that this manipulation gave rise to an interesting dissociation between arousal at the subjective level (that was increased in the happy compared to the neutral mood group; see also Bakic et al., 2015), and tonic activity as measured at the autonomic nervous system (ANS) level using SCL (that was not different between the two mood groups). Importantly, the lack of SCL difference between the two mood groups could not be explained by the absence of normal and differential ANS reactions detected in our participants since they did respond stronger to response errors compared to FH, as captured by the concurrent SCR measurement. However, the lack of group difference in tonic activity (SCL) should be interpreted with caution in the present case because the elected experimental design and task demands used may have obscured a

systematic change in SCL with happy mood. One factor likely accounting for this dissociation pertains to the way the measurement was made. While the subjective ratings were performed immediately after the mood induction, the (objective) skin conductance level was defined as the mean throughout the task. It has been shown previously that the induced arousal, but not valence, decreases over time (Gomez, Zimmermann, Schär, & Danuser, 2009), which has been explained as a down-regulation of physiological arousal that interferes with task performance. At any rate, it appears plausible to conclude that the specific happy mood state elicited by the MIP in our study was not unspecific or undifferentiated, but instead, it likely corresponded to genuine joy or pleasure (i.e., a state of well-being characterized by contentment), as opposed to other positive mood states, such as bliss, euphoria or conversely serenity, ataraxis, for which arousal related changes in the ANS are likely to be observed (Christie & Friedman, 2004; Shiota, Neufeld, Yeung, Moser & Perea, 2011). As a limitation, we note however that because participants reported an increased level of both happiness and pleasantness following the MIP, the specific mood induced probably lacked clear differentiation in terms of positive emotion content experienced by them.. Nevertheless, our attempt to specify the actual mood state elicited by the MIP, based on both subjective ratings and objective (psychophysiological) measurements, is important because positive emotion or affect is usually not conceived as an unitary construct, but it likely encompasses different forms or expressions (spanning from astonishment to euphoria), each of them being susceptible to influence cognition, physiological responding, motivation or behavior in a specific way (Shiota et al., 2014). In fact, as our behavioral results clearly show, the elicited joy in the happy mood group did not interfere with cognitive control or inhibition “directly” (as well as post-error adjustments) since behavioral performance was matched between the two mood groups (see Vanlessen et al., 2015 for a similar conclusion). This observation is important because it confirms that the idiosyncratic joy or contentment experienced by the participants (in the happy mood group) was not merely bringing noise or distraction (Dreisbach & Goschke, 2004), but it did however alter the subjective

experience of specific events, namely response errors, as revealed by the corresponding ERP results. From a methodological point of view, the balanced behavioral performance between the two mood groups is valuable because the differential error monitoring seen at the ERP level between them can therefore not be accounted by asymmetries in the number of responses errors or the speed with which they were committed, two factors that reliably influence the shape and morphology of response-locked ERP components, especially the ERN/NE (Gehring et al., 1993; Olvet & Hajcak, 2009). Noteworthy, the lack of group differences at the behavioral level (speed and accuracy) was not odd in the present case, but expected given the specifics of the Go/NoGo task used. Since the RT deadline was calibrated and updated at the single subject level, it inevitably led to a comparable number of response errors (and balanced speed) between the two groups, as already reported in previous studies using the same task and between-subjects experimental design (see Aarts & Pourtois, 2010; Aarts et al., 2013; Koban, Brass, Lynn, & Pourtois, 2012; Rigoni, Pourtois, & Brass, 2015; Walentowska, Moors, Paul, & Pourtois, 2016).

A novel and important result of our study is that despite the balanced behavioral performance between the two mood groups, the experience of joy did influence error monitoring, in a component specific fashion however. While the ERN component was similar between the groups, i.e. early error detection mechanisms remained impermeable to positive mood, the Pe component was reliably diminished in the happy compared to the neutral mood group. This effect was visible at the scalp level using both standard component/peak measurements, as well as a complementing topographical ERP mapping analysis. Furthermore, we found, using source localization methods, that this effect was likely caused by a decreased activation in a network comprising posterior cingulate and insular cortices. The contribution of these specific brain regions to the generation of the Pe component was already shown previously (Dhar, Wiersema, & Pourtois, 2011; Herrmann, Römmler, Ehlis, Heidrich, & Fallgatter, 2004; Mathewson, Dywan, & Segalowitz, 2005; Van Veen & Carter, 2002). Several authors have put forward the notion that the Pe component might reflect the processing of the motivational significance of

response errors (Leuthold & Sommer, 1999; O'Connell et al., 2007; Overbeek et al., 2005; Ridderinkhof et al., 2009; Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010). In this context, errors are considered as salient events (because they are deviant and usually worse than expected events), eliciting an "automatic" orienting response (Notebaert et al., 2009) and activating a ''salience network'', where the anterior insular cortex (and its reciprocal anatomical connections with the ACC) plays a critical role (Inzlicht, Bartholow, & Hirsh, 2015; Seeley et al., 2007; Uddin, 2014; Ullsperger et al., 2010). For example, error monitoring was found to be heightened at the Pe level selectively during placebo analgesia (Koban et al., 2012), suggesting that this specific state likely increases the motivational significance of errors while happy mood conversely appears to decrease it. In light of this evidence, it is therefore plausible – but somewhat speculative at this stage- to assume that the experience of joy or contentment could very well transiently decrease the otherwise heightened salience usually associated with error commission. Importantly, we can rule out the possibility that this effect results from a dampened reaction to response errors in happy relative to neutral participants in general. First, the post-error slowing, which is thought to reflect an unspecific attention orienting to (deviant) response errors (Notebaert et al., 2009), and is increased by (subjective) arousal (De Saedeleer & Pourtois, 2016), was preserved in the happy mood group. Second, the ANS reaction to errors, as captured by the SCR, was preserved in happy participants. Third, when controlling statistically for changes in SCL (tonic arousal) using an ANCOVA, the Pe component to response errors was still found to be reliably blunted in the happy compared to the neutral mood group. Therefore, we conjecture that the experience of joy/contentment in adult healthy participants likely alter the subjective evaluation of response errors (and more specifically, their perceived salience) rather than the arousal or ANS reaction to them. When considering the assumption of mood congruency effects (Rusting, 1998; Sharot, Korn, & Dolan, 2011; Tamir & Robinson, 2007), it is therefore possible that happy mood elicited in our study did "shield" participants from negative (mood incongruent) information, such as response errors. This could be

achieved by down-regulating their salience or meaning (at the Pe level), thereby fostering the pursuit and maintenance of the (pleasant) mood state currently experienced by the participant. Hence, happy mood could provide participants with an adaptive mechanism that seeks to conserve the benefits associated with the current mood state, which has been related to building up additional resources and protecting from the experience of stress or negative affect (Fredrickson, 2004; Schwarz & Bless, 1991). In such a state of joy or contentment, there is presumably no need to enhance or trigger alertness to response to errors since the environment in which they happen is regarded as "safe" and errors forfeit therefore their negative motivational significance or salience. Because this Pe effect related to the induction of happy mood was observed in the absence of any change at the behavioral level (compared to the control condition with a neutral mood content), and since no direct evidence is provided concerning a possible change in the actual motivational or emotional processing of errors with happy mood in this study, further research is however needed to corroborate this assumption more directly. In this context, the use of priming methods meant to explore the motivational or emotional value of actions, including errors (e.g. see Aarts et al., 2012), might be valuable.

The observation of a component-specific effect during error monitoring triggered by joy or contentment, at the Pe level, and the direction of this neurophysiological effect (namely, a reduced Pe amplitude) are worth discussing further. Interestingly, previous ERP studies already reported decreased Pe amplitude during error monitoring in depression or trait-related negative affect (Aarts et al., 2013; Alexopoulos et al., 2007; A. J. Holmes & Pizzagalli, 2010; Olvet et al., 2010; Schrijvers et al., 2009; Schroder et al., 2013),which can be considered – with some reservation however since trait and state effects do not always produce comparable changes in PM – as the opposite mood state compared to the emotion (transiently) experienced in the happy mood group in this study, yet with a similar electrophysiological effect seen in both cases. Although puzzling, this similar neurophysiological effect found in two opposite mood states could actually reflect different underlying processes or mood-

dependent alterations in these two cases. While in the case of depression (and trait negative affect), a reduced Pe is often interpreted as reflecting an inability to timely adapt or change cognitive control functions in response to negative events (or perhaps reflecting impairments to consciously register them, see Frank, D'Lauro, & Curran, 2007; Hajcak, McDonald, & Simons, 2003b; Nieuwenhuis et al., 2001), such an interpretation appears difficult to hold in the case of happy mood and positive emotions given that they usually promote (but not undermine) creativity, flexibility, and perhaps even augment cognitive control in specific circumstances (Fredrickson, 2004; Nadler et al., 2010). Interestingly, our new findings are also compatible with an earlier ERP study showing decreased Pe amplitude with relaxed mood (following a social meal) (Sommer, Stürmer, Shmuilovich, Martin-Loeches, & Schacht, 2013), suggesting that a reduced Pe with positive affect (conceived as a state) could be observed across different contexts or task settings. More generally, our new ERP results cast doubt on the assumption that a reduced Pe during error monitoring necessarily denotes decreased cognitive control during error monitoring and/or is a (neurophysiological) landmark of negative affect. Similarly, the lack of a modulation of the ERN with positive mood in our study is also informative, given that amplitude variations of this early error-related component have often been linked to negative affect and internalizing traits or disorders in the past (Hajcak et al., 2003b, 2004; Luu et al., 2000; Wiswede, Münte, Goschke, et al., 2009). We previously reported an enhanced ERN amplitude in a positive mood state, when errors were embedded in a reinforcement learning context (Bakic et al., 2014). However, in this study errors likely acquired a different meaning than in the present case, where they rather reflected attentional lapses or break down of impulse control. Hence, it appears that positive mood is versatile and can produce different effects during error monitoring depending on specific contextual or situational cues or task demands (Huntsinger, 2012). It can either increase (at the ERN level) reward prediction error when errors serve as potent learning signals (Bakic et al., 2014), or alternatively, lower

their motivational significance or salience (at the Pe level) when they provide clear challenges of self-efficacy, as found in our current study.

Some limitations warrant comment. First, although sLORETA is an empirically well supported source localization technique (Mulert et al., 2004; Pizzagalli et al., 2004; Zumsteg, Friedman, Wennberg, & Wieser, 2005), the inverse solutions obtained should be interpreted with caution because these mathematical reconstructions necessarily remain imprecise and they suffer from a low spatial resolution. Second, because the Pe was previously associated with error awareness (see Nieuwenhuis et al., 2001; Ullsperger et al., 2010), changes not only in error detection or monitoring , but also in error awareness as a function of happy mood should be evaluated more systematically in the future. The reduced Pe component found in the happy mood group in our study is unlikely to be explained by a change in error awareness in this group however, because almost all (99%) response errors are usually consciously detected by all participants in this speeded Go/NoGo task (see Vocat et al., 2008), and a normal post-error adaptation was found in both groups in the present case. Third, we observed a relatively large CRN component in our study. However, this result was not unexpected, but very much in line with previous ERP studies using the same speeded Go/NoGo task with a very strict time pressure and updated RT deadline (Vocat et al., 2008). These conditions necessarily increased uncertainty at the time of key press given that performance was based on both accuracy and speed (Walentowska et al., 2016). As a matter of fact, (enhanced) uncertainty also increases the CRN component (Coles et al., 2001; Falkenstein et al., 2000; Gehring et al., 1993). Accordingly, it remains to be tested whether effects of (positive) mood might also be observed at the ERN level, when uncertainty (regarding accuracy and/or speed) is kept low. Last, although we tried to measure and control levels of arousal in the two mood groups, subjective arousal was still larger after the MIP in the happy compared to the neutral mood group (despite the use of physical activity-related memories during guided imagery in this latter group), while the objective arousal (skin conductance as a measure of automatic arousal) was comparable

between the two groups. Even though arousal was unlikely to explain the modulation of the Pe component with happy mood in our study (see here above and results section), future studies are needed however to assess the specific contribution of (subjective and objective) arousal vs. valence (during the experience of a specific mood state) to error monitoring brain functions.

In conclusion, our results show that an emotional state induced and characterized by joy or contentment can reliably alter and presumably lower the motivational significance or salience of response errors inadvertently committed during a speeded Go/NoGo task, with effects visible at the Pe level selectively (as opposed to the preceding ERN/Ne component that remained impermeable to these mood changes). This neurophysiological effect, which does not correspond simply to a blunted arousal reaction to errors with happy mood, likely stemmed from a reduced activation in the anterior insula and posterior cingulate cortex (as confirmed by complementing source localization results), which are presumably both involved in the processing of the salience of these worse than expected events. Therefore, we conclude that the transient experience of joy or contentment in healthy adult participants does not merely interfere with cognitive control, inhibition or automatic error detection (reflected by the ERN component, or concurrent changes in the SCR), but instead, it appears to enable an adaptive and mood-congruent change in the organisms such that the (negative) meaning or impact of these unwanted events is transiently downplayed.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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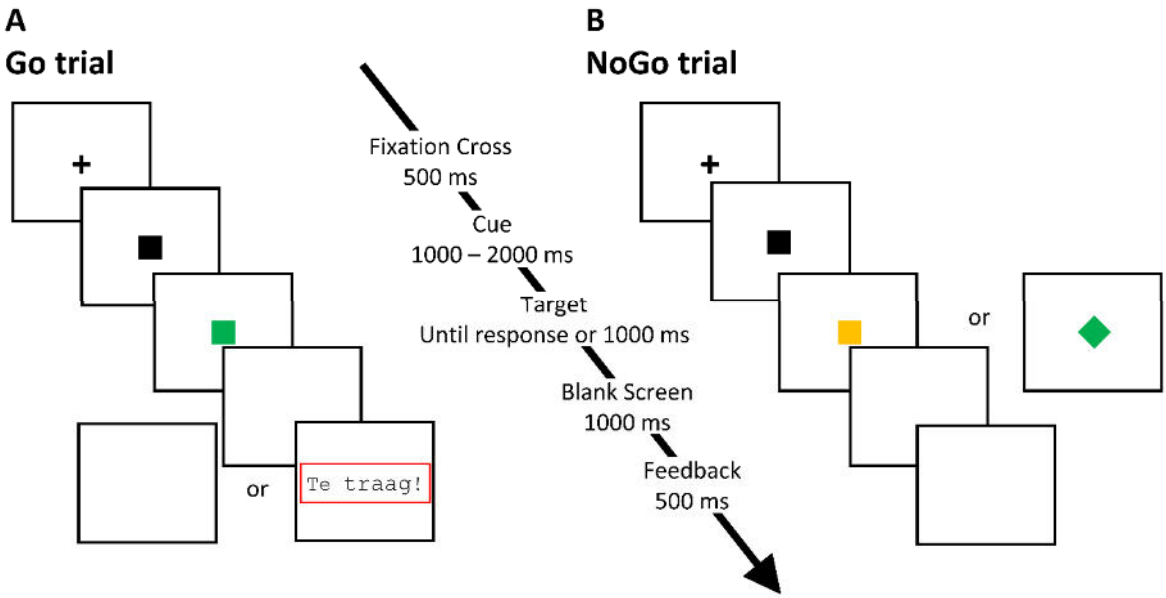


Figure 1. Stimuli and task. (A) On each trial, a black square was presented. After a variable interval (1000 ms–2000 ms), the black square (two thirds, Go trials) became green and kept its initial orientation (either square or diamond). (B) On the remaining one third of the trials, it became either orange or green but with a change in orientation (NoGo trials).

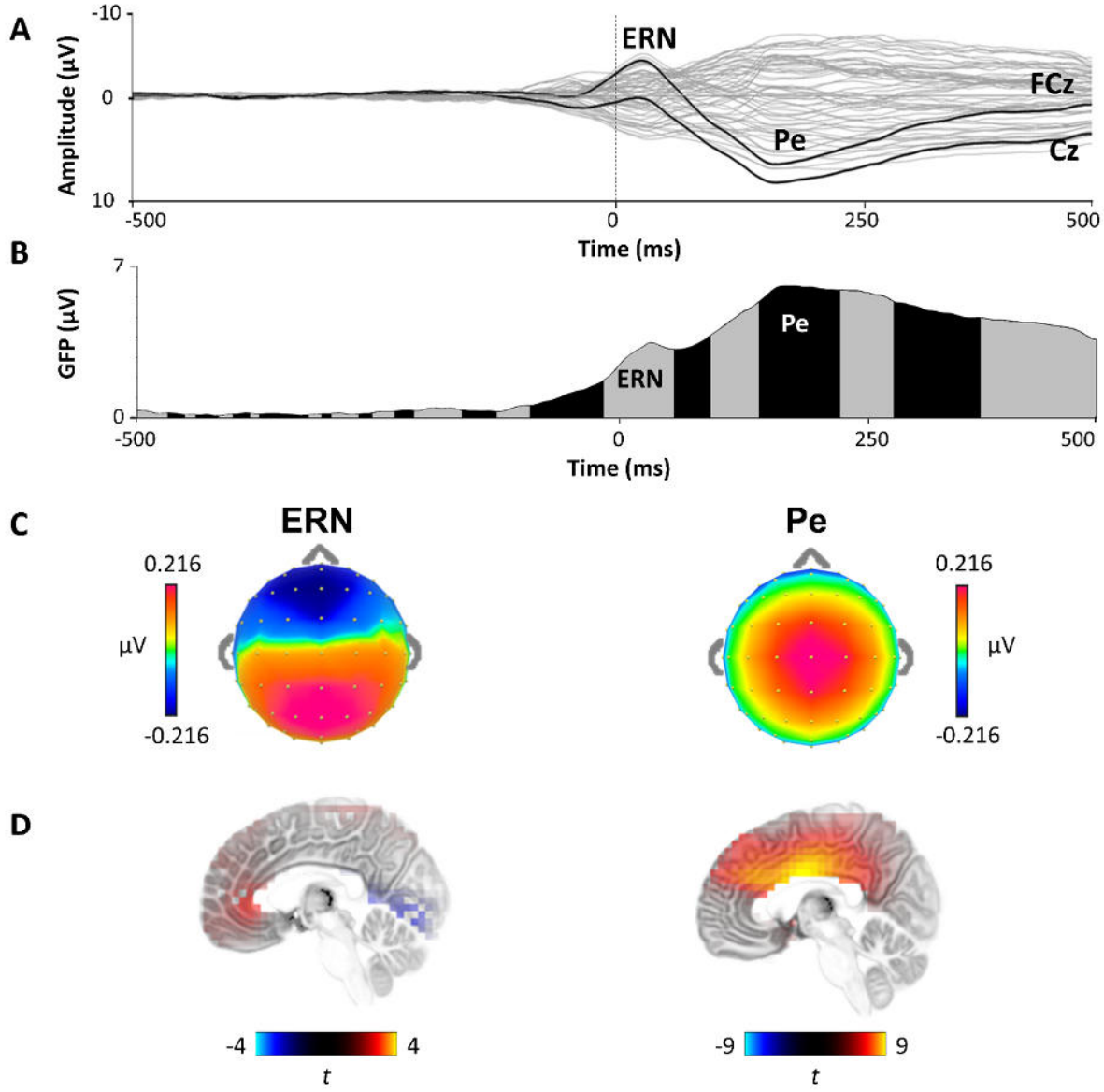


Figure 2. Main ERP results. (A) A butterfly view of the grand-average error-related ERP data in the neutral mood shows that ERN reached its maximum around 10-50 ms at FCz while the subsequent Pe peaked at 145-200 ms post-response-onset at electrode Cz. The waveforms recorded at FCz and Cz are depicted in black. (B) Result of the corresponding topographical ERP mapping analysis. Two distinct topographical maps, the ERN/Ne and Pe, were isolated using a clustering method (see methods section for details). (C) These two topographical maps unambiguously corresponded to the ERN/Ne and Pe component. (D) Using sLORETA, a direct statistical comparison between Errors and FH during the ERN time interval (left panel) showed enhanced error-related activity arising in the rostral part of the ACC, while during the Pe time interval, this error-related activity encompassed more dorsal and posterior cingulate regions

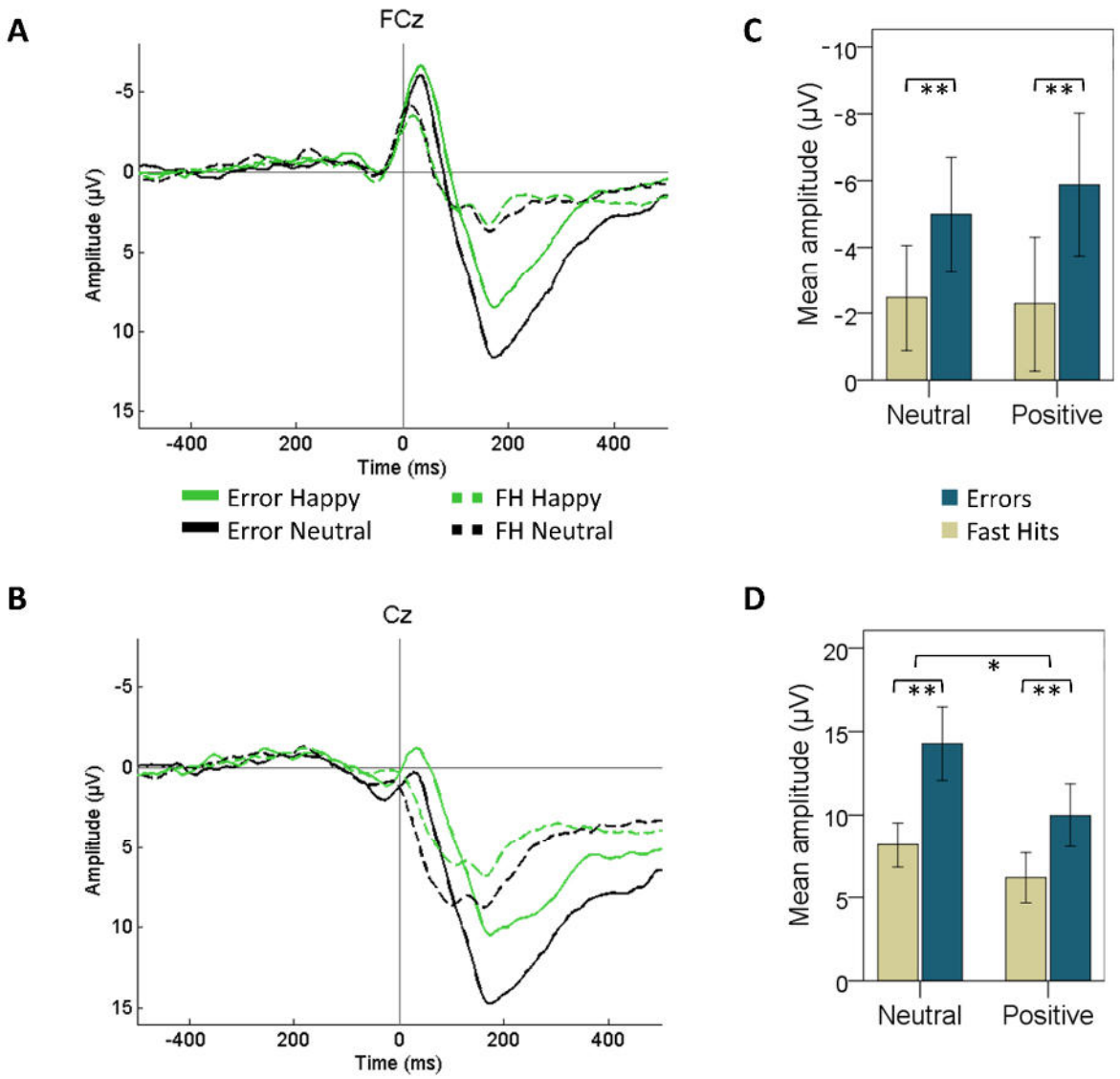


Figure 3. ERP results. (A) Grand average ERP waveforms at FCz (ERN) shown for each mood group (neutral and happy) and response type (error and FH) separately. (B) Grand average ERP waveforms at Cz (Pe) shown for each mood group (neutral and happy) and response type (error and FH) separately. (C) Mean amplitude at FCz (expressed in μV) for the ERN (errors) and CRN (hits) for the two groups separately. A significant main effect of accuracy was found whereby the ERN was larger than the CRN, equally so in the two mood groups. (D) Mean amplitude at Cz (expressed in μV) for the Pe (errors) and Pc (correct hits) for the two groups separately. Unlike the ERN, the Pe was reliably reduced in the happy mood group, as revealed by a significant group x accuracy interaction effect. The error bar represents the 95 % confidence interval (CI). * refers to $p < .05$, ** refers to $p < .001$..

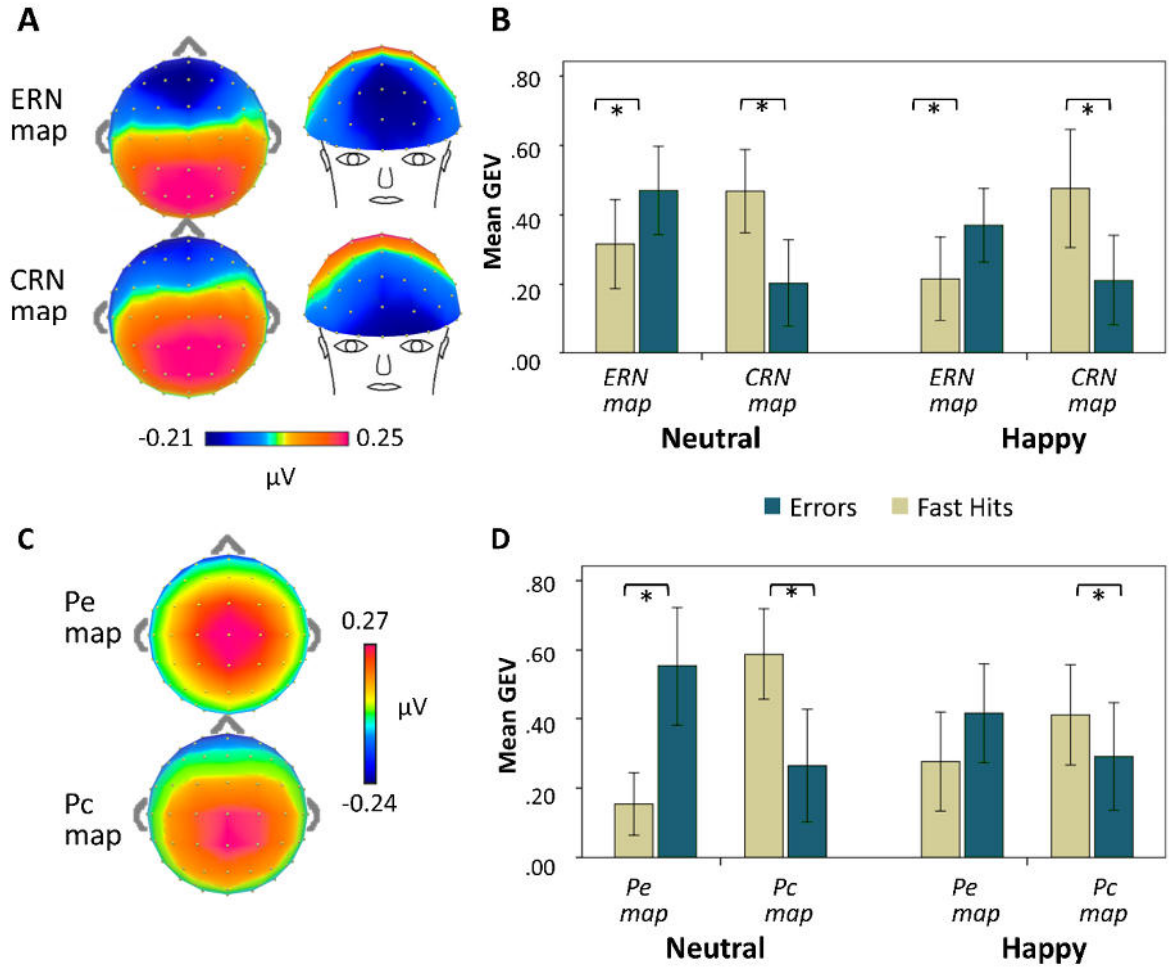


Figure 4. Results of the topographical ERP mapping analysis. (A) The scalp map of the ERN showed a negative activity over prefrontal electrodes along the midline, while the CRN had a qualitatively different scalp configuration. (B) For both groups, the ERN/Ne topographical component explained more variance for errors than hits, while the topographical component corresponding to the CRN showed the reversed pattern. (C) The scalp map of the Pe was characterized by a broad positive activity over central electrode positions whereas FH were associated with a qualitatively different scalp configuration during the same time interval (Pc). (D) The Pe topographical component explained more variance for errors than FH, but in the neutral group only (this effect was substantially attenuated in the happy mood group), while the Pc component explained more variance for FH than errors in both groups. Error bars correspond to 95 % CI. * refers to $p < .05$.

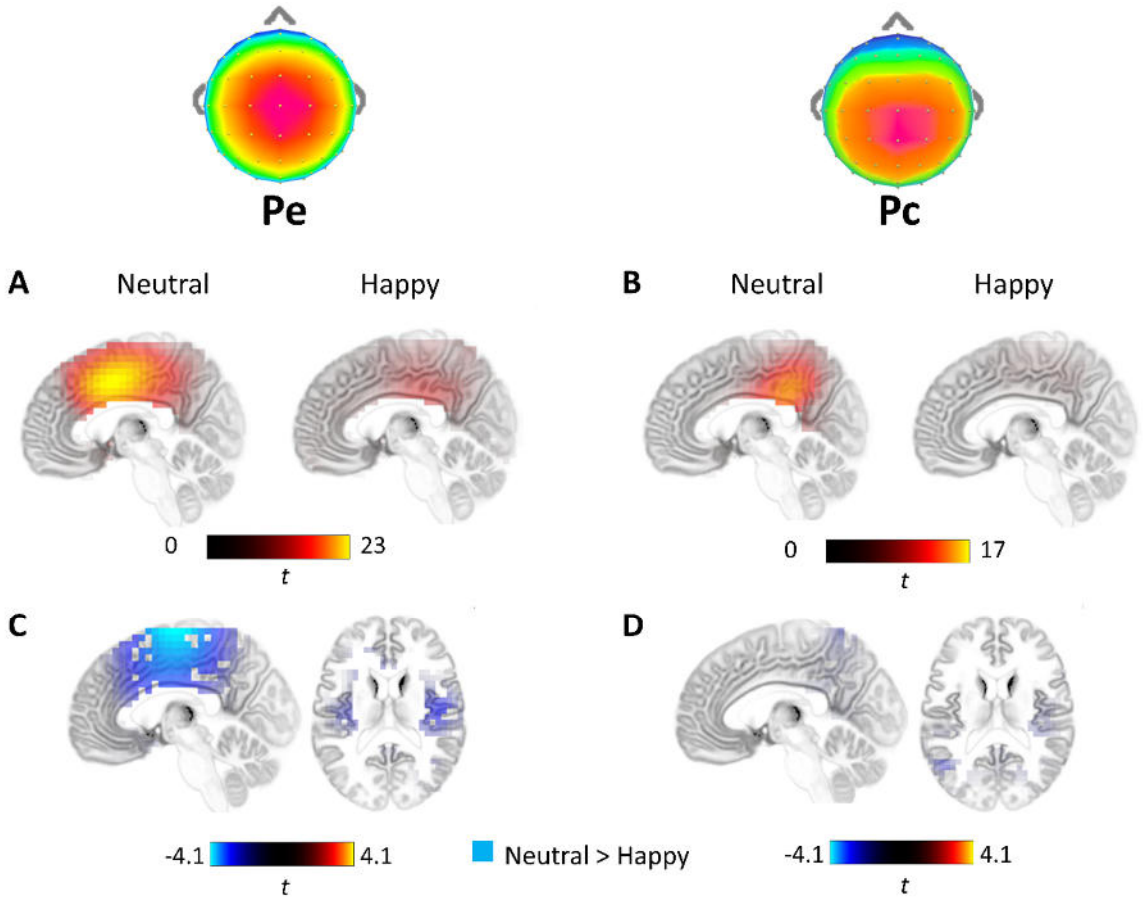


Figure 5. Source localization results (sLORETA). (A) Inverse solution for the Pe (errors) shown separately for the neutral and the happy mood group, revealing a main (and extended) cluster encompassing the dorsal ACC and posterior parts of the cingulate gyrus (BA 24), which was reliably reduced in the latter group. (B) Inverse solution for the Pc (FH), separately for the neutral and the happy mood group, revealing an overall smaller cluster (than the activity elicited for errors) in posterior parts of the cingulate gyrus (BA 31), which was less active in the latter group. (C) A direct statistical comparison between the two groups for errors revealed that the neutral group had stronger activations than the happy group within the dorsal ACC and posterior cingulate gyrus (BAs 24, 31, 6), as well as the insula bilaterally (BA 13). (D) For FH, group differences (in these same regions) were clearly more modest and circumscribed than for errors.

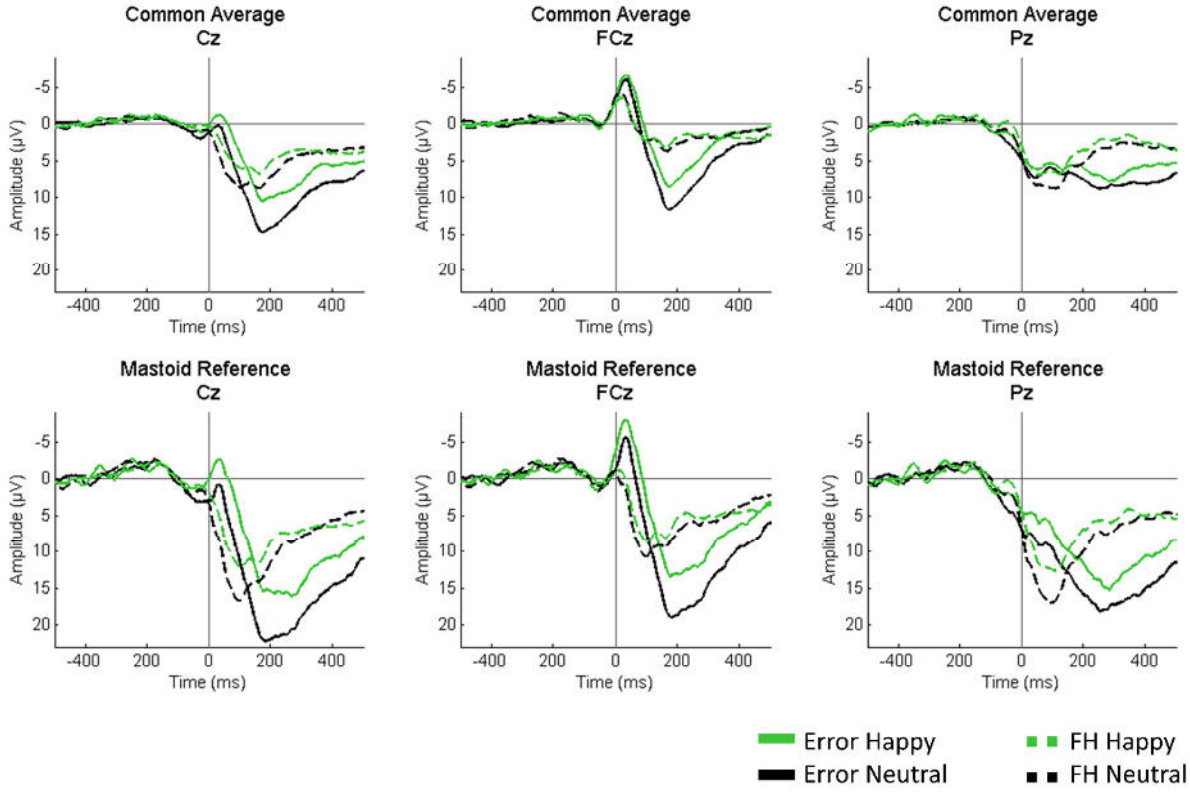
Trial Type	Neutral		Happy		Comparison		
Number of Trials per Condition							
	M	*SD*	*M*	*SD*	*t* (42)	*p*	*d*
FH	98.3	30.2	93.9	35.6	.45	.65	.12
Error	50.4	24.7	49.6	23.3	.11	.91	.001
Speed (ms) per Condition							
	M	*SD*	*M*	*SD*	*t* (42)	*p*	*d*
FH	217	34.3	215	24.2	.20	.84	.06
Error	314	44.6	321	36.0	.20	.84	.17
Post FH	258	36.0	259	29.2	.16	.87	.05
Post error	275	52.8	283	32.5	.58	.57	.17
Post-error-slowing	15.8	32.3	21.6	20.1	.71	.48	.21

Table 1. Accuracy and mean reaction times per mood group for each trial type

Neutral memories		**Positive memories**	
House & garden work	(6)	Activity with friends	(6)
Running, jogging	(5)	Sport (excitement)	(5)
Prepare food	(5)	Vacation, relaxation	(5)
Swimming	(3)	Mating Behavior	(4)
Walking, hiking	(3)	Buy wanted thing	(3)
Riding bike	(2)	Family	(2)
Moving flat	(1)	Childhood memory	(1)

Table 2. Content of the reported memory. Participants in the neutral mood group used sport-related activities (in line with the instructions), while the ones in the positive mood group retrieved activities

including primarily a social component.



Supplementary Figure 1. Additional analyses showed that the use of average mastoids, as opposed to the common average reference, did not change the main outcome of the study (i.e., happy mood influences the Pe component selectively).